Seasonal variability of forest sensitivity to heat and drought stresses: A synthesis based on carbon fluxes from North American forest ecosystems

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Abstract

Climate extremes such as heat waves and droughts are projected to occur more frequently with increasing temperature and an intensified hydrological cycle. It is important to understand and quantify how forest carbon fluxes respond to heat and drought stress. In this study, we developed a series of daily indices of sensitivity to heat and drought stress as indicated by air temperature (T_a) and evaporative fraction (EF). Using normalized daily carbon fluxes from the FLUXNET Network for 34 forest sites in North America, the seasonal pattern of sensitivities of net ecosystem productivity (NEP), gross ecosystem productivity (GEP) and ecosystem respiration (RE) in response to T_a and EF anomalies were compared for different forest types. The results showed that warm temperatures in spring had a positive effect on NEP in conifer forests but a negative impact in deciduous forests. GEP in conifer forests increased with higher temperature anomalies in spring but decreased in summer. The drought-induced decrease in NEP, which mostly occurred in the deciduous forests, was mostly driven by the reduction in GEP. In conifer forests, drought had a similar dampening effect on both GEP and RE, therefore leading to a neutral NEP response. The NEP sensitivity to T_a anomalies increased with increasing mean annual temperature. Drier sites were less sensitive to drought stress in summer. Natural forests with older stand age tended to be more resilient to the climate stresses compared to managed younger forests. The results of the Classification and Regression Tree analysis showed that seasons and ecosystem productivity were the most powerful variables in explaining the variation of forest sensitivity to heat and drought stress. Our results implied that the magnitude and direction of carbon flux changes in response to climate extremes are highly dependent on the seasonal dynamics of forests and the timing of the climate extremes.

KEYWORDS; climatic stresses, drought, eddy covariance technique, FLUXNET2015, forest carbon cycle, heat wave, net ecosystem productivity

1 INTRODUCTION

Forest ecosystems play an important role in the global carbon cycle by taking up about 30% of the global fossil fuel carbon emissions, and therefore play an important role in regulating the atmospheric carbon dioxide concentration and stabilizing the global climate system (Luyssaert et al., 2007; Malmsheimer et al., 2011; Pan et al., 2011). The carbon exchange processes between forest and the atmosphere are controlled by climate variables such as temperature and precipitation on a daily and seasonally basis (Charney et al., 2016; Yi et al., 2010), and can have carry-over effects on processes in subsequent years with normal climate (Thomas et al., 2009). Superimposed on that, climate extremes can have a profound impact on forest carbon fluxes and their potential feedbacks to the climate system (Reichstein, Bahn, & Ciais, 2013; Schlesinger et al., 2016). Most of the interannual variability of carbon fluxes in undisturbed forests is dominated by climate extremes (Zscheischler, Mahecha, et al., 2014).

Climate extremes such as heat waves and droughts are projected to occur more frequently in the future with increasing temperature and intensified hydrological cycle (IPCC, 2014). In Europe, a severe drought and heat wave caused forest ecosystems to lose as much carbon in the summer of 2003 as had been sequestered during the previous 5 years (Ciais et al., 2005; Reichstein et al., 2007). The Amazon rainforest lost 1.2–1.6 Pg C biomass during the intense drought in 2005 (Phillips et al., 2009). In 2012, a warmer spring and severe summer drought in the eastern temperate forests of North America caused a net reduction in carbon sequestration due to the rapid depletion of soil water content (Pan & Schimel, 2016; Wolf et al., 2016). An increasing frequency and severity of climate extremes highlight the need to quantitatively understand the response of forest carbon balance to climate extremes and its variability over time and space (Berner, Law, & Hudiburg, 2017; Frank et al., 2015).

However, the response of forest carbon fluxes to climate anomalies highly depend on the seasonal timing of the climate extremes (Sippel, Zscheischler, & Reichstein, 2016; Xiao, Liu, & Stoy, 2016). High temperature in early spring may stimulate carbon sequestration by extending the growing season, but high-temperature events in summer may have negative effects on forest growth by exacerbating water deficit, and may lead to earlier leaf senescence in the autumn or reduced leaf area in the following year (Kelly, 2016; Walker, Mack, & Johnstone, 2015; Wolf et al., 2016; Xie, Wang, Wilson, & Silander, 2018). The sensitivity of forest carbon fluxes to climate anomalies may have substantial seasonal variation (Angert et al., 2005). In addition, forest type, climate, topography, stand age, and management strategy are all potential factors that determine sensitivity of the forests to climate constraints (von Buttlar et al., 2018). Moreover, the impact of heat

and drought stress could be confounded with the seasonal variation in both climate variables and carbon fluxes, as well as long-term changes such as global warming and natural forest growth (Fang et al., 2014). In order to compare the impacts of climate stresses at different sites, sensitivity indices at time scale finer than yearly are needed for quantifying the sensitivity of carbon fluxes and their seasonal variation. The controlling variables of these sensitivity indices are also needed to be thoroughly examined.

In this study, we used carbon fluxes and meteorological data from 34 forest sites having long-term measurements in North America from the FLUXNET Network database to develop daily indices of sensitivity to air temperature and dryness anomalies. These indices were used to address the following questions: (a) How do the sensitivities of forest carbon fluxes to temperature and dryness anomalies change over seasons? (b) How do the sensitivities of temperature and dryness anomalies differ among different climates, productivity, stand ages, and management strategies? (c) Which variables better explain the variation of forest sensitivity to temperature and drought anomalies among sites? The availability of longer time series of carbon fluxes through FLUXNET Network dataset has provided an opportunity to address these questions about forests' sensitivity to climatic stresses.

2 METHODS

2.1 Data sources

Carbon fluxes and meteorological data measured by the eddy covariance (EC) method from the FLUXNET Network, in particular, the FLUXNET2015 dataset (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset) was used in the analysis (Baldocchi, 2014; Pastorello et al., 2017). Half-hourly EC data were quality controlled, u^*-filtered and gap-filled following the standardized protocols (Papale et al., 2006). At each site, net ecosystem exchange (NEE) was measured and net ecosystem productivity (NEP) was obtained as –NEE. Gross ecosystem productivity (GEP) and ecosystem respiration (RE) were estimated using flux partitioning algorithms, where RE was estimated using nighttime NEE versus temperature relationships (Reichstein et al., 2005). Half-hourly data were aggregated to daily, monthly, and annual fluxes. In this study, the gap-filled daily data was used to calculate the sensitivity indices. For those sites where the valid measurements do not start at the beginning of a calendar year, the data for the first year was removed to ensure that only the completed years of measurements are used in this analysis.

To represent seasonality and the impact of climate anomalies, long-term measurements were needed to quantify heat and drought sensitivities. In this study, forest sites with at least 5 years of continuous measurements of carbon fluxes and meteorological data were selected. In the FLUXNET2015 dataset, 29 sites met this criterion. Data from additional five AmeriFlux sites that had long-term data records but were not part of FLUXNET2015 dataset (CA-Ca1, CA-Ca2, CA-Ca3, US-Bar, and US-Ho1) were also included in this

analysis. The data was processed using the same methodology used in the FLUXNET2015 (Pastorello et al., 2017). In total, 34 sites from North America were used in this study, with 351 site-years of data (Table 1; Figure 1). Eight sites were broadleaved deciduous forests (DBF), twenty-two were evergreen needle-leaved forests (ENF), and three were mixed forests. The stand age ranged from 6 to 400 years, within which four sites are younger than 20 years and six are older than 120 years.

TABLE 1 Sites used in this study

Site ID	Latitude	Longitude	Elevation (m)	MAT (°C)	MAP (mm)	KOEPPEN Climate zone	Vegetation types	Age group	Disturbance	GEP (Mg C ha^{-1} $year^{-1}$)	Start year	End year	Reference
CA-Ca1	49.87	−125.33	300	9.93	1,369	Cfb	ENF	Mature	N	24.17	1999	2010	Humphreys et al. (2006)
CA-Ca2	49.87	−125.29	175	9.86	1,474	Cfb	ENF	Young	N	8.13	2001	2010	Humphreys et al. (2006)
CA-Ca3	49.53	−124.90	170	9.94	1,676	Cfb	ENF	Middle	N	15.90	2002	2010	Humphreys et al. (2006)
CA-Gro	48.22	−82.16	340	1.3	831	Dfb	MF	Mature	N	10.71	2004	2013	McCaughey, Pejam, Arain, and Cameron (2006)
CA-Man	55.88	−98.48	259	−3.2	520	Dfc	ENF	Old	N	6.40	1994	2008	Dunn, Barford, Wofsy, Goulden, and Daube (2007)
CA-NS1	55.88	−98.48	260	−2.89	500	Dfc	ENF	Old	N	7.94	2001	2005	Goulden et al. (2006)
CA-NS2	55.91	−98.52	260	−2.88	500	Dfc	ENF	Mature	N	8.37	2001	2005	Goulden et al. (2006)
CA-NS3	55.91	−98.38	260	−2.87	502	Dfc	ENF	Middle	N	6.63	2001	2005	Goulden et al. (2006)
CA-NS5	55.86	−98.49	260	−2.86	500	Dfc	ENF	Young	N	8.36	2001	2005	Goulden et al. (2006)
CA-Oas	53.63	−106.20	530	0.34	429	Dfc	DBF	Mature	N	11.06	1996	2010	Griffis et al. (2003)
CA-Obs	53.99	−105.12	629	0.79	406	Dfc	ENF	Old	N	8.51	1999	2010	Griffis et al. (2003)
CA-Qfo	49.69	−74.34	382	−0.36	962	Dfc	ENF	Mature	N	6.71	2004	2010	Bergeron et al. (2007)
CA-SF2	54.25	−105.88	520	0.4	470	Dfc	ENF	Young	Y	13.08	2001	2005	Amiro et al. (2006)
CA-TP1	42.66	−80.56	265	8	1,036	Dfb	ENF	Young	N	8.55	2003	2014	Arain and Restrepo-Coupe (2005)
CA-TP2	42.71	−80.35	184	8	1,036	Dfb	ENF	Young	N	23.19	2003	2007	Peichl et al. (2014)
CA-TP3	42.77	−80.46	212	8	1,036	Dfb	ENF	Middle	N	14.84	2003	2014	Peichl, Arain, & Brodeur (2010) and Peichl, Brodeur, et al. (2010)
CA-TP4	42.71	−80.36	184	8	1,036	Dfb	ENF	Mature	Y	14.40	2002	2014	Chan et al. (2018)
US-Bar	44.06	−71.29	272	5.61	1,246	Dfb	DBF	Mature	N	12.60	2005	2017	Jenkins et al. (2007)

(Continues)

TABLE 1 (Continued)

Site ID	Latitude	Longitude	Elevation (m)	MAT (°C)	MAP (mm)	KOEPPEN Climate zone	Vegetation types	Age group	Disturbance	GEP (Mg C ha^{-1} $year^{-1}$)	Start year	End year	Reference
US-Blo	38.90	−120.63	1,315	11.09	1,226	Csa	ENF	Young	N	15.15	1997	2007	Goldstein et al. (2000)
US-GLE	41.37	−106.24	3,197	0.8	1,200	Dfc	ENF	Old	Y	6.20	2005	2014	Frank, Massman, Ewers, Huckaby, and Negron (2014)
US-Ha1	42.54	−72.17	340	6.62	1,071	Dfb	DBF	Old	N	14.22	1992	2012	Barford et al. (2001)
US-Ho1	45.20	−68.74	60	5.27	1,070	Dfb	ENF	Mature	N	15.02	2012	2017	Hollinger et al. (2004)
US-Me2	44.45	−121.56	1,253	6.28	523	Csb	ENF	Mature	N	16.72	2002	2014	Irvine et al. (2004)
US-Me3	44.32	−121.61	1,005	7.07	719	Csb	ENF	Young	N	8.22	2004	2009	Irvine et al. (2004)
US-Me6	44.32	−121.61	998	7.59	494	Csb	ENF	Young	N	9.59	2010	2014	Ruehr et al. (2012)
US-MMS	39.32	−86.41	275	10.85	1,032	Cfa	DBF	Mature	Y	17.23	1999	2014	Schmid, Grimmond, Cropley, Offerle, and Su (2000)
US-NR1	40.03	−105.55	3,050	1.5	800	Dfc	ENF	Mature	N	8.44	2002	2014	Monson et al. (2002)
US-Oho	41.55	−83.84	230	10.1	849	Dfa	DBF	Mature	N	17.96	2004	2013	Xie et al. (2014)
US-PFa	45.95	−90.27	470	4.33	823	Dfb	MF	Mature	Y	9.98	1996	2014	Desai et al. (2015)
US-Prr	65.12	−147.49	210	−2	275	Dwc	ENF	Mature	N	3.91	2010	2014	Nakai et al. (2013)
US-Syv	46.24	−89.35	540	3.81	826	Dfb	MF	Old	N	13.68	2002	2014	Desai, Bolstad, Cook, Davis, and Carey (2005)
US-UMB	45.56	−84.71	234	5.83	803	Dfb	DBF	Middle	N	12.90	2002	2014	Curtis et al. (2005)
US-UMd	45.56	−84.70	239	5.83	803	Dfb	DBF	Middle	Y	14.79	2007	2014	Gough et al. (2013)
US-WCr	45.81	−90.08	520	4.02	787	Dfb	DBF	Mature	N	11.49	1999	2014	Cook et al. (2004)

Abbreviations: DBF, broadleaved deciduous forests; ENF, evergreen needle-leaved forests; GEP, gross ecosystem productivity; MAP, mean annual precipitation; MAT, mean annual temperature; MF, mixed forests. See Table S.1 for the abbreviations of KOPPEN climate zones.

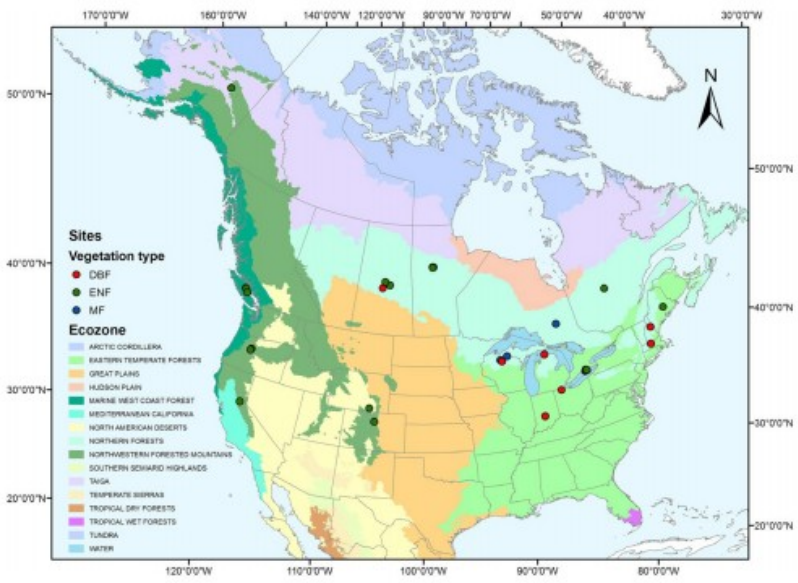

FIGURE 1 A map of North America showing the location and vegetation type of forest sites included in this study. The background color shows the ecological regions in North America (https://www.epa.gov/eco-research/ecoregions-north-america)

Daily mean air temperature (T_a) was used as an indicator of heat stress. Daily evaporative fraction (EF = LE/(LE + H)) was used as an index of drought to indicate drought stress, where LE is the latent heat flux and H is the sensible heat flux, both using daily integrated data. EF is a dryness index that is driven by the variation of precipitation, soil moisture, and temperature, and biophysical processes such as photosynthesis and transpiration (Schwalm et al., 2010). It is widely used as an index of water deficit (Wei et al., 2014), ranging from 0 when fully dry, to 1 when fully wet. EF is a comprehensive dryness index that can represent dryness variation at daily time scale using the FLUXNET data. However, the dryness indicated by EF in the wet regions could be overestimated during the wet season. The limitation of EF is further addressed in the discussion.

2.2 Sensitivity index

The impacts of extreme events may potentially be masked by interannual climate variability, forest growth, and mean seasonal climate cycle. Data normalization processes help to separate the effect of periodic climate extremes from long-term climate trends. Therefore, each of the daily time series of carbon fluxes (NEP, GEP, and RE) and environmental variables (T_a and EF) for each of the sites were detrended and normalized in two steps. First, a linear regression curve was fitted for each variable against the number of days in the study period, and the regression curve predicted value was subtracted from the original daily data in order to remove the effect of long-term climatic change (in environmental variables) and forest growth relative to size (in carbon fluxes variables). Second, a multiyear 5 day moving average of daily data was used to calculate the multiyear mean value for each day, which was then subtracted from the value of the corresponding day for each year to estimate anomalies. The anomalies data

were normally distributed with a mean of zero in all the variables and the original unit of each variable was kept.

After the normalization process, the daily anomalies of environmental variables and carbon fluxes from multiyears were pooled together for every 15 day period for each of the 34 sites. The correlations between each pair of environmental variables and carbon fluxes within each of the 15 day moving-window were analyzed using linear least square regression method. When the correlation was significant ($p < .05$), the slope of the linear relationships demonstrates the direct effect of climate constraints on the carbon fluxes (Schwalm et al., 2010; Wu & Chen, 2013) and it is comparable among different sites and months with a standard unit of g C m^{-2} day^{-1} $°C^{-1}$ for T_a, and g C m^{-2} day^{-1} for EF. Therefore in this study, the slopes of the regression between carbon fluxes and T_a and EF anomalies were used as a series of daily indices of heat and drought sensitivities. Heat stress was indicated by increasing T_a, but drought stress was indicated by decreasing EF. To unify the sensitivity indices for heat and drought stress, the slopes of EF and carbon flux anomalies were multiplied by −1. Therefore negative values in both T_a and EF sensitivity indicate that heat and drought stress significantly decreased carbon fluxes in this study. The width of the moving-window (15 days in this analysis) was determined by a sensitivity analysis using data from CA-TP4 and US-MMS sites. Testing with a window size ranging from 7 to 30 days, the 15 day moving-window allowed the preservation of the seasonal variation of the sensitivity indices while providing a sufficient sample size for the regression analysis.

2.3 Data analysis

A series of site-level variables were used to explain the seasonal pattern of carbon fluxes sensitivities to T_a and EF anomalies. The forest type, climate zone, mean annual temperature (MAT), mean annual precipitation (MAP), latitude, longitude, and elevation of the site were obtained from the AmeriFlux general information dataset (AA-Flx-BIF). All the sites were classified into four age classes: young, middle, mature, and old growth. Primary forests and naturally regenerated secondary forests were defined as natural forests. Planted and managed forests were defined as managed forests. Forests that experienced disturbance such as fire, selective thinning, pest, and pathogen damage within the past 20 years before the measurements were classified as disturbed sites. Considering the differences in phenology in eastern and western North America, sites were separated into eastern and western regions with the longitude of −105° considered as a separation line (Buotte et al., 2019). Age class, management status, and disturbance history were assigned to each of the sites based on the site descriptions from the published references. Mean annual total GEP was used to represent the productivity of the sites. The seasons were defined by calendar months, according to the Koeppen climate zone for each of the sites (see Table S1 for the definition of seasons in each climate zone). The growing season included all the months in spring, summer, and autumn.

The daily curves of T_a and EF sensitivities of NEP, GEP, and RE were compared among different forest types. There were 23 ENF sites in the study, therefore the sample size was large enough to separate the eastern and western sites in the comparison. The correlation between the daily NEP sensitivities and the daily mean T_a, precipitation and vapour pressure deficit (VPD) were tested separately using linear regression analysis for spring, summer, and autumn. The bin-average values for NEP, GEP, and RE were calculated to show the general trend. The daily sensitivities indices were averaged into seasonal based on the definition of seasons for each site (Table S1). The correlation between site productivity (represented by mean annual GEP) and the seasonal mean of T_a and EF sensitivities were tested for spring, summer, and autumn. The seasonal sensitivities of natural and managed forests and forests of different age classes were compared.

To conduct a comprehensive analysis of the controlling factors of the sensitivities to temperature and drought anomalies, a multivariate analysis that can reflect nonlinear and nonadditive relationships is needed. We used a Classification and Regression Tree (CART) analysis for the T_a and EF sensitivities of NEP at seasonal timescale. CART is a nonparametric statistical method to explain the variation of a single response variable based on continuous and categorical explanatory variables (De'ath & Fabricius, 2000). The trees explain the variation of the response variable by repeatedly splitting the data into more homogeneous groups using combinations of explanatory variables. It can identify relatively important relevant variables regardless of the variable distribution and independence (Li et al., 2016; Zhang, Wu, et al., 2017) CART's ability to handle nonlinear relationships, strong interactions, and missing values made it a useful tool to analyze complex ecological data, especially in the synthesis of multisites data (Mika & Keeton, 2013; Nunery & Keeton, 2010). In this study, the response variables were the seasonal T_a and EF sensitivities of NEP. The explanatory variables included in the analysis were forest type, season, age class, management status, disturbance history, eastern or western geographic location, site elevation, MAT, MAP, and mean annual GEP. The minimum number of data points in each leaf was set up to 15 to control the depth of the regression trees in this methodology. Predictor importance of all the explanatory variables was calculated to compare the relative predictive strength of all the variables. All the calculations and analysis were conducted in MATLAB software (The Mathworks Inc.).

3 RESULTS

3.1 Seasonal patterns of temperature and drought sensitivities in evergreen and deciduous forests

The daily pattern of T_a and EF sensitivity of the DBF and ENF in eastern and western Northern America are shown in Figure 2, with negative sensitivity values representing heat or drought stress (e.g., $dNEP/dT_a < 0$). In the early spring, the mean of NEP sensitivity to T_a was greater than 0 in the ENF

(Figure 2c,e), but smaller than 0 in the DBF (Figure 2a), indicating stronger spring heat stress in deciduous forests. In the summer, most of the eastern ENF sites showed decreasing GEP with T_a anomalies ($dGEP/dT_a < 0$) when DOY was around 200, while RE increased with T_a anomalies ($dRE/dT_a > 0$ in Figure 2c). Therefore, the mean T_a sensitivity of NEP was negative in eastern ENF in the summer. The same pattern was observed in the western ENF (Figure 2e). The average summer T_a sensitivity of NEP was around -0.18 g C m^{-2} day^{-1} $°C^{-1}$, suggesting a strong summer heat stress in the ENF (Figure 2c,e). In contrast, the GEP and RE responded similarly to T_a anomalies in the DBF during the summer days (Figure 2a). Therefore, NEP in deciduous forests was relatively less sensitive to summer heat stress ($dNEP/dT_a > 0$).

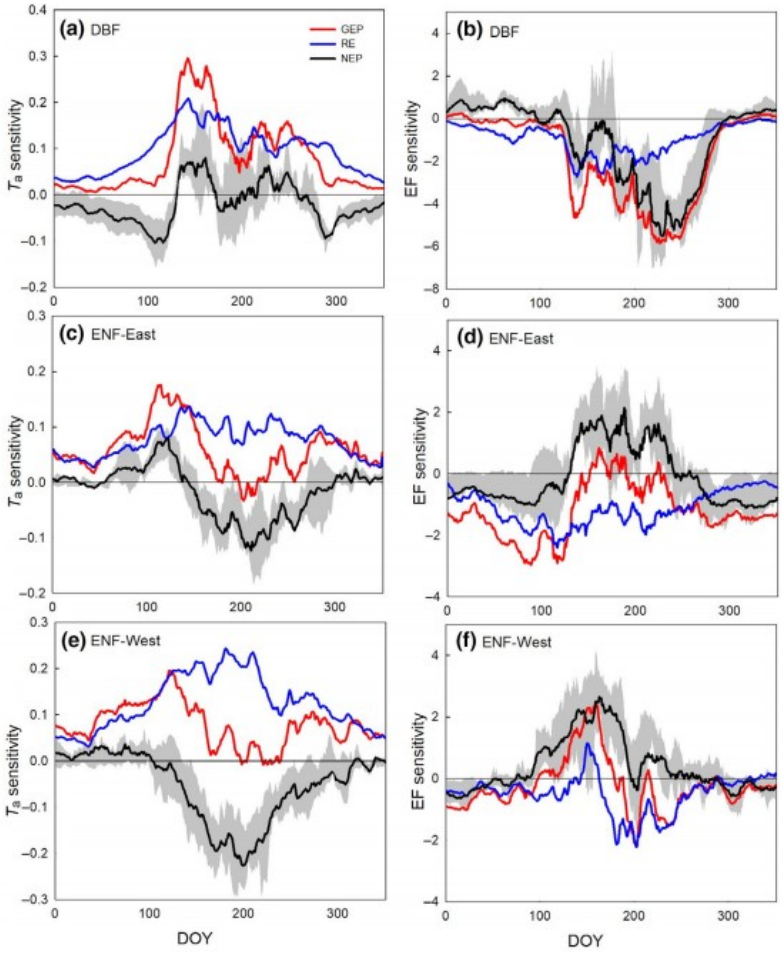

FIGURE 2 Daily sensitivities of forest carbon fluxes to air temperature (T_a, g C m^{-2} day^{-1} $°C^{-1}$) and dryness represented by evaporative fraction (EF, g C m^{-2} day^{-1}) anomalies. (a) T_a sensitivity in Deciduous Broadleaf Forest (DBF), (b) EF sensitivity in DBF, (c) T_a sensitivity in evergreen needle-leaf forest (ENF) in eastern sites, (d) EF sensitivity in ENF in eastern sites, (e) T_a sensitivity in ENF in western sites, and (f) EF sensitivity in ENF in western sites. Curves show the mean sensitivity in the 15 day moving-windows. The shaded area shows the 25% and 75% percentile of the net ecosystem productivity sensitivities among sites

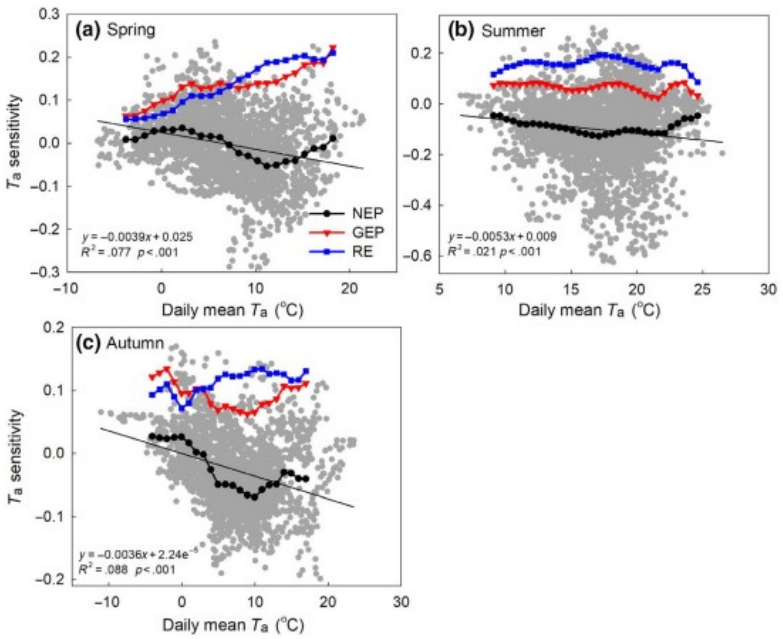

FIGURE 3 Relationships between the sensitivities of carbon fluxes to air temperature (T_a) anomalies (g C m^{-2} day^{-1} $°C^{-1}$) and mean daily T_a in (a) spring, (b) summer, and (c) autumn. Bin averages of T_a sensitivities of NEP are shown in black curves, GEP in red, and RE in blue. The bin width is 1°C for spring and autumn and 0.5°C for summer. The original data of daily NEP sensitivities are shown in gray. Significant regression relationships at $p < .01$ are shown as solid lines. GEP, gross ecosystem productivity; NEP, net ecosystem productivity; RE, ecosystem respiration

The EF anomalies had a persistent negative effect on both the GEP and RE throughout the growing season except a short period of positive effect on GEP during April and May in ENF-West. As a result, the western ENF sites showed no drought stress on NEP throughout the year (−dNEP/dEF < 0 in Figure 2f) and the eastern ENF sites only showed negative drought impact on NEP in winter (Figure 2d). In the DBF, drier conditions led to decreasing GEP in all the sites during the growing season and the impact on GEP exceed the impact on RE from July to October (Figure 2b). Therefore, the mean NEP sensitivity to EF anomalies could reach to −6 g C m^{-2} day^{-1} in summer days later in the growing season.

3.2 Climate controls on temperature and drought sensitivities

Sensitivities of NEP to T_a anomalies decreased with increasing daily mean T_a in all three seasons during the growing season (Figure 3a–c), indicating NEP in warmer conditions was more sensitive to heat stress over the growing season. Higher sensitivities of NEP to summer heat stress (more negative NEP sensitivity) were also observed in days and sites with lower daily mean precipitation and higher VPD (Figure S1b,e). A positive correlation between GEP and RE sensitivities to T_a anomalies and daily mean T_a was found in the spring (Figure 3a), but not in summer and autumn. Sensitivities of NEP to EF anomalies decreased with increasing daily mean precipitation and decreasing VPD in summer (Figure 4b; Figure S2e), indicating NEP at wetter conditions was more sensitive to summer drought stress. In spring and autumn, the EF sensitivities in NEP are not correlated with daily mean precipitation (Figure 4a,c).

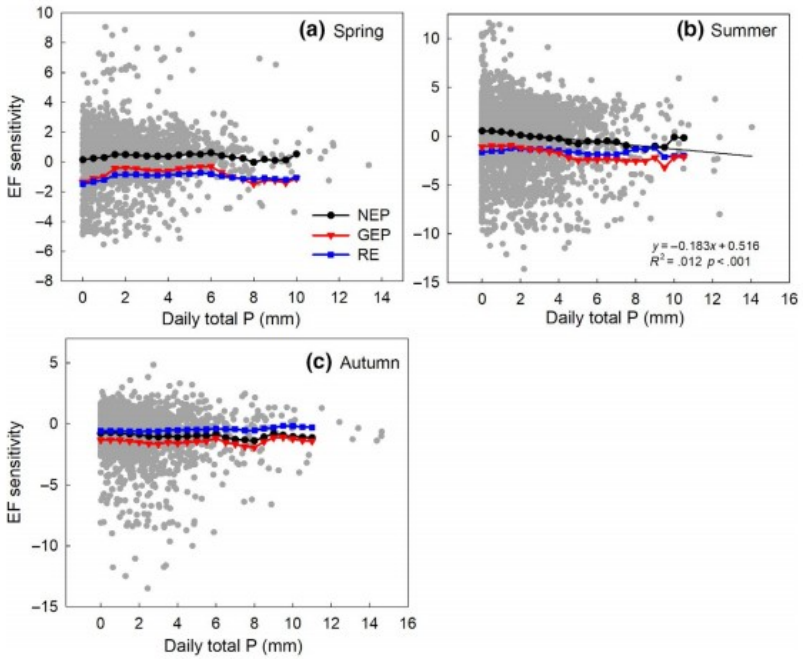

FIGURE 4 Relationships between the daily sensitivities of carbon fluxes to evaporative fraction (EF) anomalies (g C m^{-2} day^{-1}) and mean monthly precipitation (*P*) in (a) spring, (b) summer, and (c) autumn. Bin averages of EF sensitives of net ecosystem productivity (NEP) are shown in black curves, gross ecosystem productivity (GEP) in red and ecosystem respiration (RE) in blue. The bin width is 0.5 mm for all seasons. The original data of daily NEP sensitivities are shown in gray. Significant regression relationships at $p < .01$ are shown as solid lines

3.3 Other controlling factors of sensitivities

Among all the explanatory variables, forest productivity indicated by mean annual GEP of each site explained most of the variation of the seasonal NEP sensitivities to T_a and EF anomalies. The T_a sensitivities of NEP decreased with increasing annual GEP in all the seasons, while sensitivities of GEP increased with increasing annual GEP (Figure 5a–c). Sites with greater productivity tend to be more sensitive (more negative NEP sensitivity) to heat stress throughout the growing season. The seasonal EF sensitivity of NEP was positively correlated with annual GEP in spring but negatively correlated with annual GEP in summer and autumn (Figure 5d–f). Sites with greater productivity were more sensitive to summer and autumn drought stress, but less sensitive to drought stress in spring.

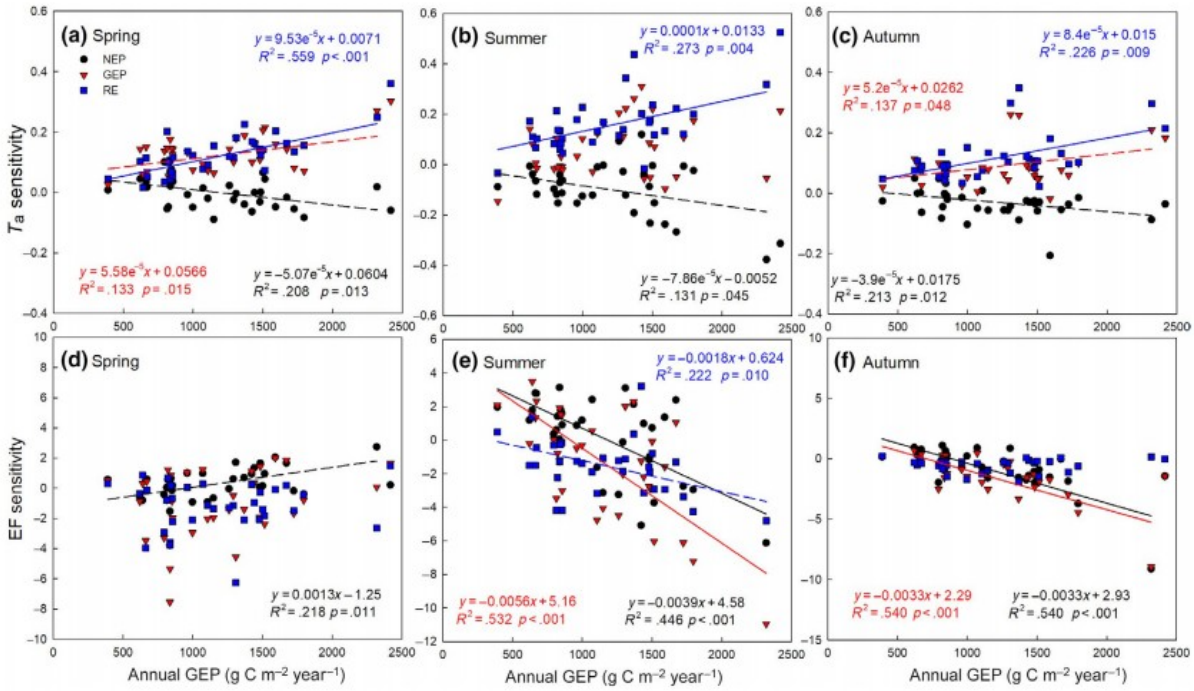

FIGURE 5 Relationships between the seasonal sensitivities of carbon fluxes to air temperature (T_a; a–c) (g C m^{-2} day^{-1} °C^{-1}) and evaporation fraction (EF; d, e) (g C m^{-2} day^{-1}) anomalies and mean annual gross ecosystem productivity (GEP) in spring (a, d), summer (b, e), and autumn (c, f). Data points and regression lines of net ecosystem productivity (NEP) are shown in black color, GEP in red and ecosystem respiration (RE) in blue. Significant regression relationships at $p < .01$ are shown as solid lines. Significant regression relationships at $.01 < p < .05$ are shown as dashed lines

In the growing season, the natural forests had relatively smaller T_a sensitivity in NEP (less negative value) compared to the managed and planted forests (Figure 6a). In managed forests, the NEP was strongly limited by abnormally higher T_a in summer (negative sensitivities), due to much greater T_a sensitivities in RE comparing with the T_a sensitivities in GEP. Generally, NEP in the natural forests was not affected by drought stress in summer. However, in managed forests, the GEP and RE were very sensitive (negative sensitivities) to drought stress throughout the year. The NEP in managed forests was strongly reduced by drought stress in summer and autumn.

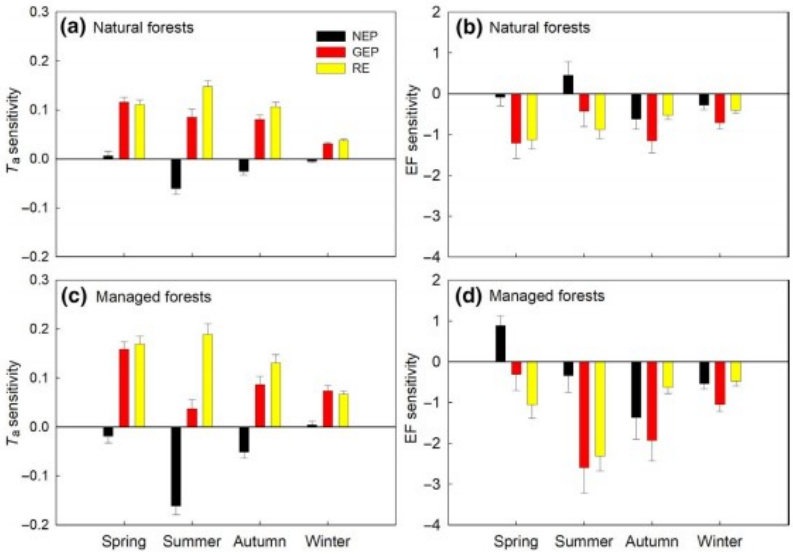

FIGURE 6 Effect of forest management on sensitivities of forest carbon fluxes to air temperature (T_a, g C m^{-2} day^{-1} °C^{-1}) and evaporative fraction (EF, g C m^{-2} day^{-1}) anomalies. The seasonal T_a and EF sensitivities of net ecosystem productivity (NEP), gross ecosystem productivity (GEP), and ecosystem respiration (RE) in natural (a, b) and managed (c, d) forests were averaged and the *SE* among sites within each season is given as error bars

Sensitivities of carbon fluxes to T_a and EF varied with forest stand age. The growing season T_a sensitivity of NEP was largest in magnitude in the young forests and smallest in the old growth forests (Figure 7a). The old growth forests had greater GEP and RE sensitivity to T_a than the middle-aged and mature forests, but the impact of T_a anomalies on GEP and RE were similar, leading to a smaller NEP sensitivity. The young forests were more sensitive to drought stress in all the carbon flux variables (Figure 7b). In mature forests, the average NEP sensitivity of EF anomalies was greater than 0, showing the forests' tolerance to drought stress.

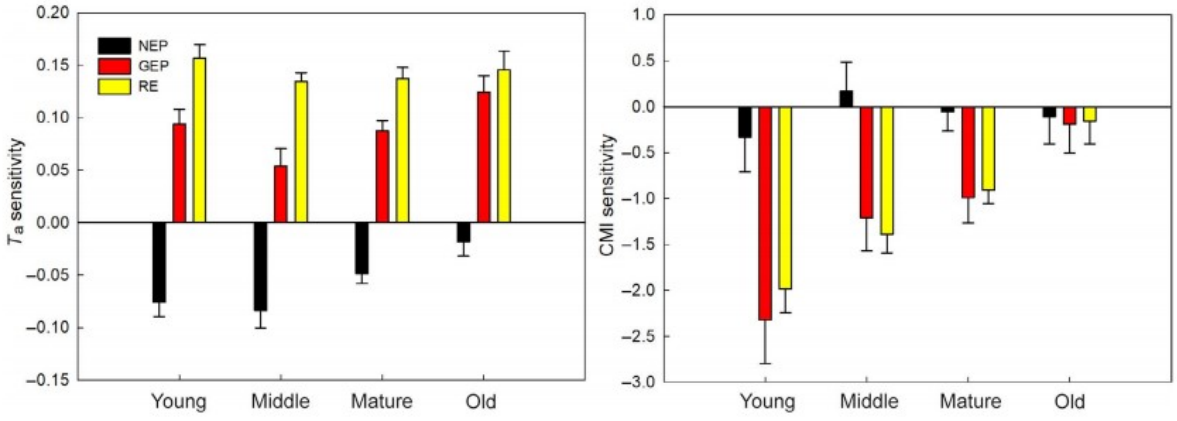

FIGURE 7 Age effect on air temperature (T_a, g C m^{-2} day^{-1} °C^{-1}) and evaporative fraction (EF, g C m^{-2} day^{-1}) sensitivities of carbon fluxes in the growing season. The mean monthly T_a and EF sensitivities of net ecosystem productivity (NEP), gross ecosystem productivity (GEP), and ecosystem respiration (RE) in young, middle-aged, mature and old-growth forests during the growing season were averaged among sites. The *SE* values within each age class are given as error bars

3.4 Using CART to explain the variation of temperature and drought sensitivities

The results of the CART analysis showed that seasonality was the most important explanatory variable in explaining the variation of the T_a

sensitivities of NEP (Figure 8a). Summer was separated from the other seasons in the first partition because of a stronger negative impact of warm temperature anomalies. Forest management status also explained deviation in NEP sensitivity, at levels less than seasonality (Table 2). Other than that, elevation, MAT, and forest type explained a small portion of the deviation. Forest productivity, MAP, forest age class, disturbance history and eastern and western geographic locations were not selected in the CART analysis of NEP–T_a sensitivity. The greatest sensitivities to heat stress (most negative values) occurred during the summer at natural forest sites.

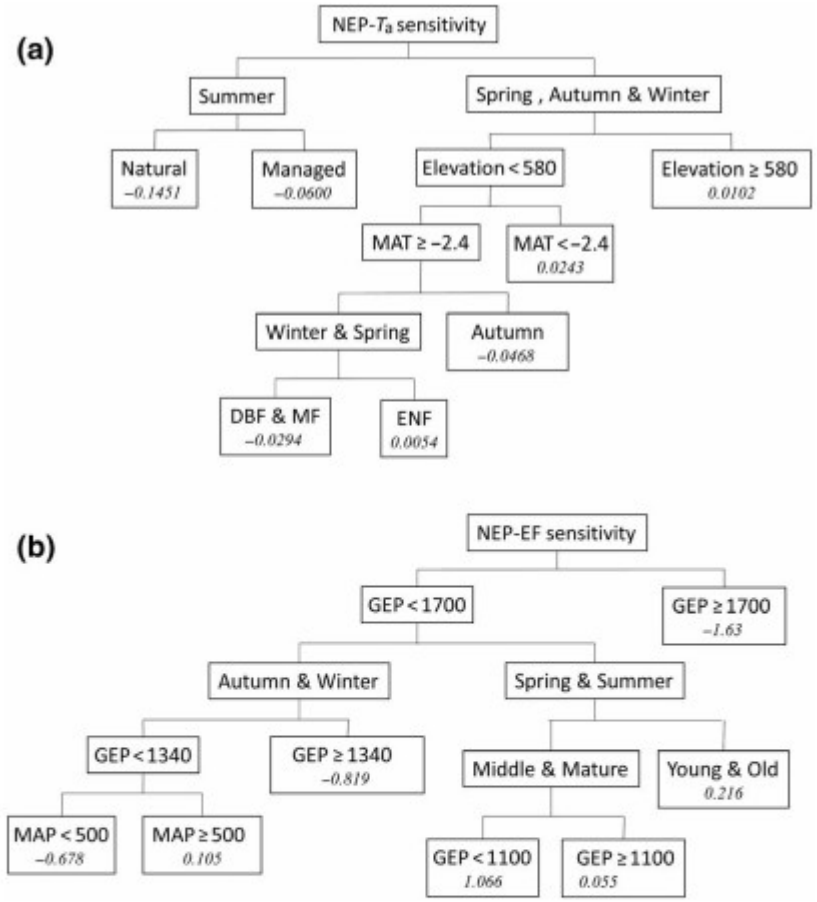

FIGURE 8 Classification and Regression Tree (CART) analysis on seasonal net ecosystem productivity (NEP) sensitivities to air temperature (T_a, a) (g C m^{-2} day^{-1} °C^{-1}) and evaporative fraction (EF, b) (g C m^{-2} day^{-1}) anomalies. The CART ranks the explanatory variables based on predictive power with the variable that explains the highest amount of variance in the dependent variable on top. The explanatory variables were selected from Table 2. Minimum node size = 15. DBF, broadleaved deciduous forests; ENF, evergreen needle-leaved forests; GEP, gross ecosystem productivity; MAP, mean annual precipitation; MAT, mean annual temperature; MF, mixed forests

TABLE 2 Predictor importance of all the explanatory variables in the CART analysis of NEP sensitivity to T_a (g C m^{-2} day^{-1} °C^{-1}) and EF (g C m^{-2} day^{-1}) anomalies. The type of the variable is also shown

Explanatory variable	Type	T_a sensitivity ($\times 10^{-4}$)	EF sensitivity ($\times 10^{-2}$)
Season	Categorical	2.47	2.20
Management	Categorical	0.74	0
Elevation (m)	Continuous	0.56	0
MAT (°C)	Continuous	0.35	0
Forest type	Categorical	0.16	0
GEP (g C m^{-2} $year^{-1)}$	Continuous	0	6.51
Age	Categorical	0	1.45
MAP (mm)	Continuous	0	0.74
Disturbance	Categorical	0	0
Eastern/Western location	Categorical	0	0

Abbreviations: CART, Classification and Regression Tree; EF, evaporative fraction; GEP, gross ecosystem productivity; MAP, mean annual precipitation; MAT, mean annual temperature; NEP, net ecosystem productivity; T_a, air temperature.

Among the 10 explanatory variables considered in the CART analysis, mean annual GEP was the strongest predictor of EF sensitivity for NEP (Figure 8b; Table 2). The primary split at the root node separated the group of very productive sites (GEP > 1,700 g C m^{-2} $year^{-1}$) with the greatest sensitivity of drought stress. The less productive sites were further divided by season, forest age, and MAP. MAT, forest type, elevation, management status, disturbance history, and eastern and western geographic location were not included in the CART model of NEP–EF sensitivity.

4 DISCUSSION

4.1 Seasonal variation of temperature and drought sensitivities

Using the long-term flux data from FLUXNET Network (e.g. FLUXNET2015) dataset, we developed a series of daily indices of forest sensitivity to temperature and dryness anomalies. The results of these indices show that the sensitivity of forest to heat and drought stresses is not consistent throughout the year. The sensitivity of the carbon fluxes depend on the seasonal timing of the stresses, as well as other site-level variables, such as forest management, stand age, and productivity status. NEP, being the difference between GEP and RE, showed a complicated seasonal pattern in

its sensitivity to climate anomalies (Figure 2). In this study, we used the seasonal dynamics of photosynthesis (GEP) and respiration (RE) and their limiting factors to interpret the sensitivities of NEP in different types of forests (Mizoguchi et al., 2012).

Our results showed that NEP in ENF decreases with T_a anomalies because the RE anomalies had consistent positive correlations with T_a anomalies throughout the growing season, but T_a sensitivity in GEP decreased to below 0 in summer months in eastern and western ENF. A well-accepted conceptual model is that, at the ecosystem level, photosynthetic response to temperature follows a quadratic function (Ma, Osuna, Verfaillie, & Baldocchi, 2017; Niu et al., 2012), while respiration increases exponentially, but declines with soil water limitations (Irvine & Law, 2002; Wen et al., 2006). Our results supported this conceptual model by illustrating that most of the ENF in North America experienced GEP decline when the temperature was higher than their optimum temperature in late summer. The temperature exceeding photosynthesis optimum temperatures may exacerbate water stress as vapor pressure deficits increase while water table decreases during the peak of the growing season (Adkinson, Syed, & Flanagan, 2011; Novick et al., 2016). However, the DBF, which is commonly adapted to a warmer and wetter environment, may not reach their thermal optimality even in the summer months. The contrasting responses of GEP and RE to T_a anomalies led to a very strong negative impact on NEP in later summer in the ENF. Evidence from site level study, tree ring record, remote sensing, and modeling results also agree that heat stress in the late summer can cause significant decline in forest growth (Buermann et al., 2014; Walker et al., 2015; Williams, Torn, Riley, & Wehner, 2014; Wu & Chen, 2013).

Another significant difference between forest types in their sensitivities to temperature anomalies is that, in early spring, NEP increases with T_a anomalies in the eastern and western ENF (positive sensitivities in Figure 2c,e), but decreases with T_a anomalies at all the DBF sites (negative sensitivities Figure 2a). It is likely that the deciduous forests did not yet develop sufficient leaf area in the early spring to respond to the increasing temperature, as compared to the evergreen forests. As a result, the slowly increasing GEP was not able to compensate the rapid increase in RE, thus the net carbon balance of the deciduous forests was strongly limited by heat stress in spring. But the effect of heat stress on NEP disappeared in the following summer as increased leaf area led to an amplified response of GEP to temperature anomalies. Other research focusing on the DBF sites also showed that heat waves that occurred during the time of leaf expansion could dramatically reduce leaf area and lead to significant carbon loss in the deciduous forest (Geddes, Murphy, Murphy, Schurman, Petroff, & Thomas, 2014).

The daily indices of T_a sensitivities developed in this study provide a good opportunity to quantitatively understand forests response to heat stress at a finer time scale. In a global synthesis, von Buttlar et al. (2018) concluded

that heat stress had only small or virtually zero impact on GEP in both ENF and DBF, resulting in a reduction in NEP as RE increase with temperature. However, our results showed that the photosynthetic response to temperature anomalies could be very different among different seasons. In our study, 14 (out of 21) ENF sites experienced significant GEP decline with increasing temperature for more than 10 days during summer. Since the study conducted by von Buttlar et al. (2018) did not consider the timing of the heat waves, it is very likely that the negative heat impact in summer was offset by the positive impact in spring, resulting in a neutral response of GEP to heat stress in ENF over the yearly basis.

The seasonal dynamics of carbon fluxes and their sensitivities to drought stress are tightly coupled with soil water availability and stomatal activity (Thomas et al., 2009). During drought stress, when soil moisture is inadequate to meet the water demand of carbon assimilation, stomatal closure and reduced mesophyll conductance may lead to a decline in photosynthesis (Rennenberg et al., 2006). At the same time, the lower soil water content may limit soil respiration and its response to soil temperature changes (Jassal, Black, Novak, Gaumont-Guay, & Nesic, 2008; Wen et al., 2006). In our results, drought stress indicated by EF anomalies has a negative effect on GEP and RE at almost all the sites and seasons. This negative impact of drought stress was stronger in summer and autumn. A recent analysis based on tree ring data found that drought extremes during the dry season had a greater impact on forest growth (Huang, Wang, Keenan, & Piao, 2018). In our analysis for North American sites, most of the forest stands experienced relatively dry periods during summer and autumn. It is likely that the soil water availability could drop to a level that suppressed both assimilation and respiration during the climatic dry season. The forest ecosystem which was limited by energy in the early growing season, switched to be limited by water availability in the later growing season, and the water limitation could be further exacerbated when the climatic drought was overlapped with the peak of forest growth and water consumption through transpiration (Fisher et al., 2007).

In the ENF, the drought impact on NEP was near neutral during the growing season. That is because the GEP and RE responded to EF anomalies in a very synchronous way. A multisite interannual analysis (Doughty et al., 2015) and a warming and precipitation controlled experiment (Suseela & Dukes, 2013) illustrated that drought reduced root autotrophic respiration possibly due to loss of root conductivity in dry periods (Domec, Warren, Meinzer, Brooks, & Coulombe, 2004). Root respiration is a major component of RE and is tightly correlated with photosynthesis (Peichl, Brodeur, Khomik, & Arain, 2010). Research from other ENF forests emphasizes the coupling of above- and belowground processes to their sensitivity to drought stress (Phillips et al., 2016; Ruehr, Martin, & Law, 2012). Similar results reported at site level studies (Allard, Ourcival, Rambal, Joffre, & Rocheteau, 2008) and global synthesis of ENF (Schwalm et al., 2010) also showed that the synchronous

response of GEP and RE to summer drought result in a neutral impact on net carbon balance in the ENF.

In the DBF, GEP was more sensitive to EF anomalies than RE in the late summer and autumn, resulting in a significant decrease in NEP under drought stress. This result agreed with the site-level analysis, which showed that the drought caused greater suppression of GEP than RE, due to the reduction of leaf conductance and leaf area in a deciduous temperate forest (Noormets et al., 2008). Severe drought may induce leaf shedding or early leaf senescence during the late growing season in DBF (Ruehr, Gast, Weber, Daub, & Arneth, 2016; Sperlich, Chang, Penuelas, Gracia, & Sabate, 2015). In contrast, the ENF, especially the pine-dominated forests were able to maintain a higher water use efficiency under drought stress, and possibly benefitting from a deeper root system in conditions that the shallow soil water is depleted (Gao et al., 2017). It should be noticed that most of the ENF sites with long-term flux measurements were dominated by pine species (9/13 sites in the east and 6/10 sites in the west), while the DBF sites were various in their species composition. Our results provide new evidence that the sensitivity of carbon fluxes to drought stress depend on species composition and plant functional traits in forests (Anderegg et al., 2018; Welp, Randerson, & Liu, 2007).

4.2 Controlling factors of temperature and dryness sensitivities

Climate variables such as mean daily temperature and precipitation had a moderate impact on the sensitivities of carbon fluxes to climate anomalies. Generally, NEP of warmer sites/months were more sensitive to heat stress in all the seasons. The strongest coupling between NEP sensitivities and mean daily temperature was observed in autumn. The lower soil water content in autumn can partly explain the seasonal hysteresis of sensitivities change in response to temperature (Niu et al., 2011; Reich et al., 2018). The stronger heat stress response in warmer sites and seasons further implied that a warmer climate as predicted in the future might shift the temperature sensitivity to a higher level, therefore aggravating the impact of heat extremes through a positive feedback (Charney et al., 2016). The T_a sensitivity was also greater in the drier sites and months in the summer (Figure S1b), suggesting that the forest sensitivity to temperature variations was regulated by moisture conditions (Wang et al., 2014).

In our study, sites/days with less precipitation had relatively smaller EF sensitivity in summer. As mentioned previously, summer is the relatively dry season for most of the North American sites. It is likely that forests in drier condition had adapted to the frequent droughts during the late growing season by the synchronous response to GEP and RE. Therefore these drought-tolerant forests were able to maintain a conservative carbon balance in the dry season (Suseela & Dukes, 2013).

Our results provided clear evidence that planted or managed forests were more sensitive to climate anomalies than the natural forests. Many studies

had reported the significant negative impact of heat and drought events in planted forests (Goldstein et al., 2000; Migliavacca et al., 2009; Sun, Wen, Yu, Liu, & Liu, 2006). Comparisons between managed forests and their counterpart natural forests also revealed that their response to the same extreme event could be opposite (van Gorsel et al., 2016; Zald & Dunn, 2018). Other studies have indicated that resistance of forests to climate extremes is determined by the species composition and stand density (Arthur & Dech, 2016; Giuggiola, Bugmann, Zingg, Dobbertin, & Rigling, 2013). Natural forests with lower density, higher structural complexity, and more understory tend to be more resilient to climate anomalies. It is also implied that sustainable forest management strategies have the potential to reduce the impact of climate extremes in managed forests.

The sensitivities of carbon fluxes to climate anomalies also change with stand age. Our results showed that the younger forests were most sensitive to heat and drought stress. It was also suggested by a comparison between an old-growth and a young ponderosa pine forest, in which the young forest showed increasing stomatal resistance, decreasing water potential, and soil respiration under drought stress (Irvine, Law, Anthoni, & Meinzer, 2002). During forest development, the decreasing stand density, and increasing root volume and depth might trade-off with the increasing soil water demand and result in a general increase in resilience to heat and drought stress (Schwarz et al., 2004). Several studies based on site chronosequence showed that the ecosystem level WUE peaked at the middle-age stage (Kwon, Law, Thomas, & Johnson, 2018; Skubel et al., 2015; Tang et al., 2017). It was in agreement with our result that the middle-age sites had the lowest GEP sensitivity to temperature anomalies. However, the large site-to-site variation might weaken the specific age effect on forest sensitivities to climate stresses, as compared to the chronosequence studies (Amiro et al., 2010). Large uncertainty still existed, especially in the old-growth forests, in their response to climate extremes.

Ecosystem productivity is a biological factor that relates to many processes in carbon fluxes. Among all the site level variables the mean annual GEP, as an indicator of ecosystem productivity, explained most of the spatial variations in sensitives of temperature and dryness anomalies. Except for the positive drought impact in spring in very productive sites, our results showed that the negative impact of heat and drought stress on NEP was stronger in more productive sites in all the seasons. A global synthesis found that droughts consistently had a more detrimental impact on the growth of larger trees (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015). McNulty, Boggs, and Sun (2014) hypothesized that slower growing chronically stressed trees with smaller productivity would be more resilient to extreme episodic stress associated with future climate change. Our results agree with this hypothesis by showing that the fast-growing forests with higher productivity and more large trees were more sensitive to climate anomalies.

4.3 Modeling the sensitivities of NEP

The result of the CART analysis further demonstrated that seasons played a very important role in determining the sensitivities of carbon fluxes to climate extremes. The prediction power of season and productivity (indicated by mean annual GEP) was the highest in the regression trees of T_a sensitivity and EF sensitivity in NEP. They can explain more than 40% of the variation in the sensitivity of NEP. It was implied that studies of forest response to heat stress should consider the timing of the heat wave, the forest management status, and climatic variables; while studies of forest response to drought stress should consider the more integrated control from productivity, stand age, and phenological characteristics of the sites.

The CART analysis allowed us to simultaneously evaluate the impact of categorical and continuous variables in modeling the sensitivities of carbon fluxes and compare their predicting power (De'ath & Fabricius, 2000). However, it is not necessary that all the variables affecting forest response to climate anomalies are included in the models. Large interactions among the explanatory variables might shape the CART results. For example, natural forests have been shown to be less sensitive to drought stress than the managed forests (Figure 6). However, forest management was not selected in the regression tree, possibly because natural forests were generally older and less productive than the managed forests. The impact of forest management had been represented by other explanatory variables in the model.

This study provides a good example of how CART can be used in the multisites synthesis. As a classification method, the CART analysis has been widely applied at the landscape scale studies using spatial data (Fellman, Buma, Hood, Edwards, & D'Amore, 2017; Rothwell, Futter, & Dise, 2008; Suchenwirth, Forster, Lang, & Kleinschmit, 2013). The sensitivity indices we developed based on FLUXNET data, combining with the CART analysis provides a research framework that had the potential to extrapolate the plot level EC measurements to larger spatial scale. Our study shows that CART analysis and existing spatial databases such as topography, climate, land cover, and greenness index data can be used to map the spatial distribution of forest carbon fluxes sensitivity to climate extremes in North America.

4.4 Limitations and future efforts

The daily sensitivity indices of heat and drought stress we developed based on FLUXNET Network database still have some limitations. First of all, since the FLUXNET data had very fine time resolution (half-hourly) but not very long time series (5–21 years in this study), we were not able to consider the long-term lag effect of climate extremes on the daily indices of sensitivities. However, the climate extreme events had an impact on carbon fluxes on time scales ranging from days to months (Thomas et al., 2009; Wu et al., 2018). For example, the heat waves in the spring might not have a significant impact on forest carbon uptake in spring, but might induce GEP decline by reducing the leaf area in a DBF (Xie et al., 2018). Although our

analysis helps to quantify short-term impact of extremes (over 15 days time frame), it suggests that more long-term data are needed to quantify the lag effect of climate extremes and how forest carbon fluxes recover from the heat and drought stress (Starr et al., 2016). The daily carbon fluxes and climate anomalies in this study can be further used to quantitatively examine how climate extremes in different season determine the annual carbon balance in forest ecosystems. Secondly, many studies had indicated that the impacts of heat and drought stress on forest carbon fluxes are tightly correlated (Kelly, 2016; Zhang, Shao, Jia, & Wei, 2017; Zhang, Wu, et al., 2017; Zscheischler, Mahecha, et al., 2014; Zscheischler, Michalak, et al., 2014). In fact, the impact of heat stress was dominated by heat-induced water stress, which was mediated by soil moisture availability (Duarte et al., 2016; Reich et al., 2018; Walker et al., 2015). In our data, the daily T_a and EF anomalies were correlated in almost all the sites, while the daily sensitivities of T_a and EF are not correlated. The purpose of our analysis was not to compare between heat and drought stresses in their impact on carbon fluxes, but to quantify the sensitivity of these two stresses in a systematic way, therefore to compare the sensitivity of both of the stresses in and among different seasons. The carbon fluxes and climate anomalies we developed in this study can be further used to test the compounding effect of heat and drought stresses caused by concurrent extreme events. Thirdly, the dryness indicated by EF in this study could be overestimated in some northeast sites, as the LE was limited by radiation during the growing season (Teuling et al., 2009). As a result, the EF sensitivity in wet days could be overestimated in these sites. More accurate dryness index at daily timescale is needed to improve the estimations of forest sensitivity to drought stress. Finally, in this study, the GEP and RE data based on nighttime fluxes were used to calculate the climate sensitivities. The air temperature was one of the variables that was used to extrapolate the daytime data, therefore daily T_a tended to be correlated with daily GEP and RE (Vickers, Thomas, Martin, & Law, 2009). The autocorrelation between T_a and fluxes data may lead to overestimation of GEP and RE sensitivity to T_a anomalies. Precaution should be taken in interpreting the T_a sensitivities. Further research is needed to evaluate the impact of data processing methods on studies about forest response to climate extreme events.

5 CONCLUSIONS

Using the daily meteorological and carbon flux data from 34 sites across North America from the FLUXNET Network dataset, we developed a series of daily indices of sensitivity to heat and drought stress as indicated by T_a and EF, respectively. Heat waves in spring had a positive impact on NEP in ENF but a negative impact in DBF. Summer heat led to GEP reduction, resulting in significant NEP decline in ENF. The drought-induced decrease of NEP mostly occurred during late summer in the DBF, and they were driven by the reduction of GEP in most of the sites. In ENF, drought had a similar dampening effect on both GEP and RE, therefore leading to a neutral NEP

response. The sensitivity of NEP to temperature anomalies increased with mean daily temperature. The sensitivity of NEP to dryness anomalies increased with precipitation in summer. Forest with older stand age, low stand density, deeper root system, and more complicated stand structure, tended to be more resilient to the climate stresses throughout the growing season, compared to younger forests. Managed forests were more sensitive to the heat and drought stress than the natural forests. Sites with greater productivity were more sensitive to heat and drought conditions in summer and autumn. The results of the CART further demonstrated that seasons played an important role in determining forest response to climate extreme. Ecosystem productivity was the most powerful variable in explaining the variation of NEP sensitivity to drought stresses.

Our results implied that the magnitude and direction of carbon flux change in response to climate extremes highly depend on the seasonal dynamics of forests, and the timing of the climate extremes. The sensitivity indices and research framework developed in this study can provide benchmarks for modeling forest response to climate extremes in a changing climate. Further research is needed to combine the sensitivity indices and CART results with spatial databases to extrapolate the site-level measurements of carbon fluxes to the continental scale, and to provide detailed seasonal variations of forest carbon flux sensitivity to climate extremes in North America.

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